

*ENHANCEMENT OF CONDITIONED AUTONOMIC
RESPONSES IN MONKEYS WHEN PRESOCK SIGNALS
OCCASION OPERANT SUPPRESSION*

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Classical pairings of a sound stimulus with shock elicited larger magnitude and more rapidly conditioned autonomic responses when subjects were responding on variable-interval schedules for food than when they were eating freely available food. The difference was not attributable to changes in control values of heart rate and blood pressure, or to alterations in motor activity, but appeared related to operant suppression.

Key words: conditioned suppression, heart rate, blood pressure, classical conditioning, respondents, autonomic responses, lever, monkeys

The conditioned emotional response (CER) that develops during a preaversive warning stimulus is in reality a shifting collection of many conditional responses, ranging from overt behavioral disruption to normally unseen physiological changes. The actual composition of the CER on any specific occasion depends on many factors, including the extent and nature of the subject's prior experience with the warning signal, the relative speed at which the different constituent responses condition and extinguish, the species of the subject, and, as well, its ongoing behavioral activities. As examples, in nonhuman primates and dogs the suppression of appetitively maintained operant responding induced by a pre-shock signal is coupled with large elevations in heart rate and blood pressure (Brady, Kelly, & Plumlee, 1969; Stebbins & Smith, 1964), whereas in rabbits (Swadlow, Hosking, & Schneiderman, 1971), rats (de Toledo & Black, 1966), and pigs (Dantzer & Baldwin, 1974) consistent patterns of bradycardia accompany operant suppression. So, too, "freezing" responses, intuitively associated with fright and originally proposed as an explanation of operant suppression itself (Hunt & Brady, 1951), typically occur in rats only on early trials, rarely on later ones (Millenson & Dent, 1971), and only infrequently appear in other species

at any point in conditioning (Kelly, 1973a, p. 102).

Although conditioned to the same warning stimulus (CS) through pairings with the unconditioned stimulus (US), the varying components of the CER are not necessarily related to each other in a causal manner. Some, such as conditioned changes in heart rate and blood pressure, are inevitably linked through normal physiological mechanisms, but other components appear to condition independently of one another. For instance, the behavioral and autonomic responses mentioned above do not appear to be causally related, for each response may be observed in the absence of the other at reliable points in the normal acquisition-extinction cycle of the CER. Operant suppression has invariably been found to condition with fewer CS-US pairings in both monkeys (Brady et al., 1969) and rats (de Toledo & Black, 1966; Parrish, 1967), whereas autonomic responses, once acquired, have been slower to extinguish (Brady et al., 1969). Thus, these two conditioned properties of a preshock stimulus, though normally appearing together as components of the mature CER, are experimentally dissociable.

On the other hand, to say that behavioral and autonomic responses are causally independent is not to imply that they may not interact, in much the same manner that two independently established operant performances may strongly interact when the subject is exposed to both simultaneously, as in a concurrent schedule, or in close succession,

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as in alternating components of a multiple or mixed schedule. For instance, one may interpret the data of Snapper, Pomerleau, and Schoenfeld (1969, Figure 1) as suggesting that heart rate accelerations in monkeys may be slightly larger when preshock stimuli are presented during free operant avoidance sessions, as opposed to in between sessions. Equivalent data are lacking for the appetitive operant case. However, during earlier studies dealing with preaversive and prereward conditioned suppression in rhesus monkeys (Brady et al., 1969; Kelly, 1973a, 1973b, Note 1), the magnitude of conditioned cardiac responses during 3-min long preshock CSs appeared to be unusually large and prolonged. Twenty to forty beat-per-minute (bpm) elevations over baselines of 150 to 200 bpm were not uncommon during CSs that also occasioned operant suppression, and in some subjects conditioned cardiac increases exceeding 75 bpm were sustained for a full minute or longer. Cardiac accelerations of similar intensity and duration were also reported by Stebbins and Smith (1964) for rhesus monkeys in which classical conditioning took place during concurrent operant performances. However impressive these results, particularly the sustained nature of the cardiovascular CRs during operant suppression, it is not possible to compare these studies directly with those involving classical heart rate conditioning in unoccupied rhesus monkeys (e.g., Fenz, 1972; Miller & Caul, 1969; Ramsey, 1970; Smith & Stebbins, 1965; Snapper, Kadden, & Schoenfeld, 1971) since a variety of cardiac measures, stimulus parameters and procedures have been used.

The aim of the present experiment was to compare classically conditioned cardiovascular responses elicited when rhesus monkeys were engaged in contingent responding for food and when the same subjects were not under explicit schedule control. Staddon and Simmelhag (1971) have argued that the appropriate reference situation for controlling for the effects of contingencies upon learning is not the prior spontaneous level of occurrence of the experimental behavior in the absence of all reinforcers, but rather a situation in which reinforcers are available independently of the subject's behavior. Reinforcers per se appear to alter the likelihood of certain behaviors which in turn can interact with the behaviors under study. In the present experi-

ment an analogous consideration arises in identifying an appropriate behavioral context to control for steady-state, appetitively maintained, operant performances upon which the classical conditioning procedures are superimposed in producing conditioned suppression. Because heart rate and blood pressure are sometimes elevated during feeding (Smith, Jabbur, Rushmer, & Lasher, 1960) and because idiosyncratic consummatory patterns can contribute importantly to schedule performances in monkeys (Kelly, 1974), it was decided that cardiovascular responses obtained during concurrent conditioned suppression of operant responding would be compared with those elicited while the monkeys were fed ad libitum meals. This simple feeding procedure had certain advantages over a variable-time schedule of food delivery, which under normal conditions would have better controlled the distribution of reinforcement frequency. However, both subjects in the present study were "pouch feeders," and when presented with dry chow, they would quickly mouth and store large quantities of pellets in their jowls for later chewing and swallowing (Kelly, 1974). Hence, the monkeys controlled the actual time when the pellets were eaten in both the operant and free-feeding phases of the experiment, and by employing the latter rather than a variable-time schedule, adventitious pairings of the Pavlovian CS with the delivery of food were precluded.

The results of the comparison will suggest that those preshock warning stimuli which interrupt operant responding may be accompanied by larger magnitude cardiovascular responses than those which occur during free meals.

METHOD

Subjects

Two naive male rhesus monkeys (*Macaca mulatta*) served. Monkey P weighed 5.0 kg and Monkey T, 5.5 kg at the start of the experiment.

Apparatus

Each monkey was permanently restrained in a Plexiglas primate chair enclosed within an individual sound-attenuating booth. The main houselight was a 6-W fluorescent bulb mounted on the rear wall directly behind the subject's

head. Adjacent to the houselight was a 3-ohm speaker used to present the CS, a 20-Hz clicking noise. Water was available to the monkey at all times, and was delivered in 1-sec squirts of 7 to 10 ml each through a spout mounted 10 cm to the left of its head. The monkey could obtain water by pressing a clear plastic nose key located next to the spout, on a one-press, one-squirt basis. Aside from some fresh fruit offered several times a week, all food was obtained during experimental sessions. A 2.5-cm rim was added to the neckplate to prevent food placed on it from rolling off.

During operant sessions, a response lever, enclosed within a small box and protruding 2.7 cm from it, was mounted 13 cm directly in front of the monkey. The lever was a delicately balanced telegraph key that could be activated by exerting a dead weight force of 4.0 to 6.2 g through a negligible excursion of under .5 mm, a total minimum work requirement of approximately 245 ergs (25×10^{-6} J). Food reinforcers were Dietrich and Gambrill 750-mg whole diet pellets. They were delivered through a chute located to the right of the monkey's head, and a 1-sec tone feedback accompanied every pellet delivery. Twenty-four hour behavioral scheduling and recording were accomplished with a mixture of relay and transistor equipment located in an adjacent room.

Autonomic recording. Ten to fourteen days before the first session, each monkey was implanted in the femoral artery with a chronic catheter for continuous monitoring of heart rate and blood pressure. Details of the preparation were similar to those described by Brady et al. (1969). Blood pressure recordings were obtained with a Sanborn strain-gauge transducer and two-channel recorder. An amplified electrical signal that paralleled the pressure wave was fed to a solid-state level detector which triggered upon each heart beat (Swinnen, 1967). The heart beat impulses were accumulated and printed out at 1-min intervals, synchronized with the scheduled behavioral events.

Procedure

For two 1-hr periods each day, the first from 9 a.m. to 10 a.m. and the second from 5 p.m. to 6 p.m., the main houselights in the monkey's chamber were dimmed. Since all behavioral procedures were restricted to these cued pe-

riods, they will be referred to as 1-hr sessions, even though in some phases of the experiment only a single brief trial occurred during the hour.

(A) *CS adaptation (10 sessions).* The future conditioned stimulus, a 3-min clicking noise, was presented alone in the middle (mins 30 to 33) of 10 consecutive sessions on 5 days. Just before each session, and all sessions throughout the experiment when no operant schedule was in force, 60 food pellets (or the equivalent weight, 45 g of Purina lab chow) was spread on the neckplate of the monkey's chair. The size of this free meal equaled the amount of food available to the monkey on a contingent basis during later operant sessions.

(B) *CS-US pairings (50 sessions).* The CS was terminated after 3 mins with an unavoidable, 350-msec shock to the seat of the monkey's chair. During the first 40 pairings, the shock intensity was 5 mA; during the last 10, it was raised to 10 mA. To insure independence of autonomic responses and comparability of this experiment with others (Brady et al., 1969; Kelly, 1971, 1973a), only one pairing was scheduled per session. Sessions continued twice per day, seven days per week, except for Sessions 26 through 40, which were spaced one per day alternating with meals that were signaled as usual by dimming the houselights, but during which no CS or US occurred.

(C) *CS alone (10 sessions).* The clicking noise was presented unaccompanied by shock.

(D) *Operant training.* A response lever was added to the chamber, and each monkey was shaped using food pellets as reinforcers to press the lever with a minimum of effort. Monkey P ultimately adopted a light, brushing topography with its right forepaw, similar to petting the lever. Monkey T rested its forepaw on top of the small box from which the lever protruded and used only its dangling thumb to respond on the lever. For 10 introductory sessions, every response on the lever produced a pellet of food (continuous reinforcement, or CRF). Next, both monkeys were exposed to an identical sequence of random ratio schedules that specified a uniform probability of reinforcement for every response. Reinforcement probability was progressively decreased in successive sessions from the former 1.0 (CRF) to .5, .3, .2, .1, .07, and .04. The monkeys then were switched to a variable-interval

1-min, limited-hold 7.5-sec schedule and run for 20 sessions. The limited-hold contingency required that the monkey respond within 7.5 sec after a reinforcement was scheduled by the variable-interval timer or miss that opportunity.

(E) *CS-US pairings during operant responding (45 sessions)*. CS-US pairings were reinstituted, one per session, at the lower, 5-mA shock intensity.

(F) *Lever out (10 sessions)*. The lever was removed from the chamber, food was made freely available once again as in Phase B, and CS-US pairings continued.

(G) The lever was returned to the chamber, and Phase E was repeated (10 sessions).

(H) The lever was removed from the chamber, and Phase F was repeated (10 sessions). Due to illness and an untimely death, Monkey T did not experience this phase.

RESULTS

Figure 1 presents in five-session blocks the complete cardiac and behavioral data of Monkey P. The lowest function traces the control, or basal heart rate calculated on the 3 mins preceding the CS, or on the comparable period

in sessions when no CS occurred, as during operant training. The middle ordinate shows the principal function, changes in heart rate relative to the control rate during each of the three CS minutes. The minute-by-minute averages in the leftmost panels of Figure 1 indicate that before operant training Monkey P apparently failed to develop a conditioned cardiac response despite 50 CS-US pairings. Yet, in previous similar studies (Brady et al., 1969; Kelly, Note 1), the identical CS, US, and temporal parameters of classical aversive conditioning typically resulted in a very rapid acquisition, normally in fewer than 10 to 12 pairings, of large CS increases in both heart rate and systolic and diastolic blood pressure. The sole procedural difference from the present in the latter studies was that the previous subjects were all responding on operant schedules for food while classical pairings were carried out. In the present experiment, Figure 1 shows that following operant training (middle panels), Monkey P also exhibited large, 10 to 15 bpm, heart rate accelerations to the onset of the CS whenever the latter was presented during operant sessions (second and fourth panels from the right), whereas, when the lever was removed and CS-US pairings were carried

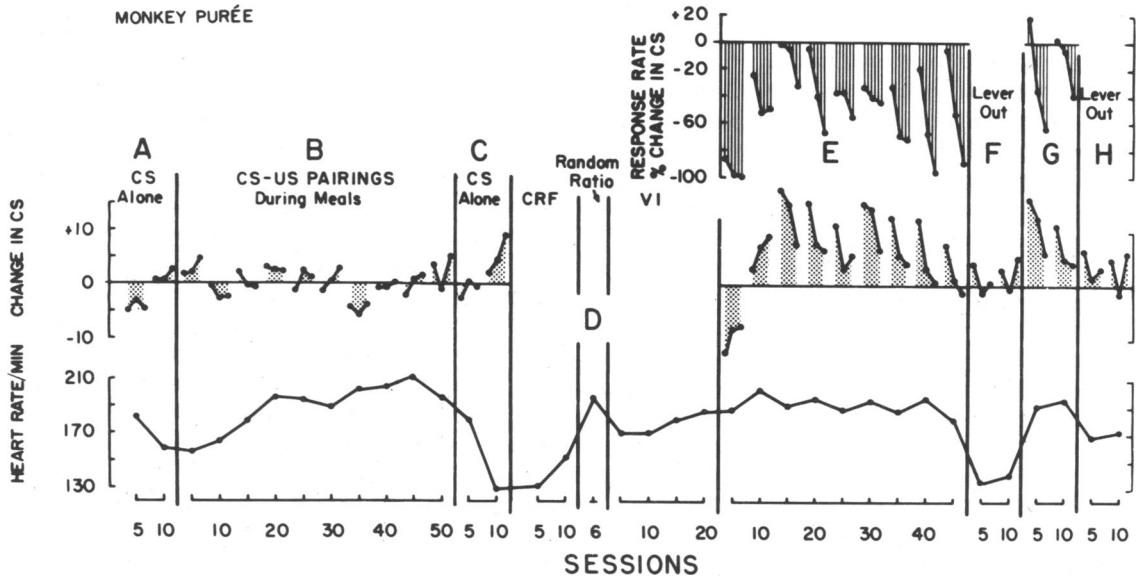


Fig. 1. Monkey P's control heart rates in bpm (bottom) and minute-by-minute deviations during the CS (middle) throughout all phases of the experiment. The zero point on the middle ordinate represents the control heart rate as calculated from the 3 mins immediately preceding the clicker. This is the same value that is plotted as the control heart rate in the bottom graph. In panels E and G to the right, minute-by-minute suppression of lever pressing is expressed in the top graph as a percent change from the pre-CS response rate calculated during the same control period. The data are averaged in 5-session blocks.

out as before with food freely available, the newly conditioned heart rate responses were sharply reduced (first and third panels from the right).

The operant data are plotted in Figure 1 on the upper ordinate directly above the corresponding heart rate responses. The measure of suppression adopted here and in Figure 3 is the percentage of change in response rate during the CS relative to the average control rate drawn from the preceding 3 mins. The percent change measure is identical, except for the decimal point, to the Hunt, Jernberg, and Brady (1952) inflection ratio, $b - a/a$, where a = control rate, and b = CS rate. The control rates of responding from which the percent change data were derived are presented in Table 1.

The behavioral data in Figure 1 are noteworthy in two respects. First, the suppression of behavior by the preshock CS was immediate and severe, with virtually complete suppression observed throughout the CS within the initial 5-trial block of Phase E. Therefore, the CS appears to have acquired its behaviorally disrupting properties during the earlier pairings with shock carried out during free meals, even though, at the time, large magnitude heart rate responses had not been evident. Second, with extended pairings the behavioral suppression eventually became temporally discriminated to the later portions of the long CS. That is, the monkey usually continued responding when the CS was presented during operant sessions, albeit at progressively slower rates as the terminal shock approached. By

contrast, over the same period it was the onset, or first minute of the CS, that elicited the most pronounced cardiac acceleration. Thus, the behavioral and cardiac accelerative responses that conditioned to the same warning signal were found to be temporally dissociated within the CS interval. With repetitions of the fixed duration CS, the behavioral suppression engendered by it showed evidence of becoming temporally discriminated within the interval, while the accelerative component of the conditioned cardiac response remained linked to the early moments of the CS. This would suggest that the behavioral and cardiac responses, though conditioned by the same environmental events, were causally independent.

Even though some parameters of the present experiment were far from optimal, such as the long CS duration, the apparent failure in Monkey P to show conditioned cardiac responses without concurrent operant responding seemed unusual in light of the several demonstrations of classical cardiovascular conditioning in unoccupied, isolated monkeys (Miller & Caul, 1969; Ramsey, 1970; Smith & Stebbins, 1965; Snapper, Pomerleau, & Schoenfeld, 1969). Figure 2 suggests, however, that Monkey P did develop conditioned responses during the early off-the-baseline phases, but that the level of analysis employed in Figure 1 (and in previous experiments) was in this instance too coarse to detect the response. Figure 2 shows the actual strip chart blood pressure recordings for selected individual trials. Starting from the top, these represent the 1st and 40th pairings during the initial off-baseline Phase B, the 21st on-baseline trial from the middle of Phase E when conditioned cardiac responses were maximal, and the final experimental trial conducted off-baseline (Phase H). Following adaptation trials but before shock pairings, the future CS had no visible effect on the monkey's blood pressure (top record). After 40 pairings with shock, taking place on a behavioral background of eating but no programmed operant responding, the onset of the 3-min CS elicited a transient increase in both systolic and diastolic blood pressure which was not sustained beyond 15 sec (second record). As a result, the minute-by-minute heart rate averages in Figure 1 did not detect the relatively small magnitude change. (A number of studies have indicated

Table 1

Pre-CS control response rates per minute during operant phases E and G.

Sessions	Monkey P	Monkey T
	Mean \pm S.E.M.	Mean \pm S.E.M.
<i>Phase E</i>		
1-5	46.84 \pm 3.59	24.82 \pm 1.47
6-10	32.52 \pm 2.93	24.96 \pm 2.11
11-15	31.94 \pm 1.62	21.24 \pm 3.77
16-20	26.66 \pm 1.39	34.54 \pm 2.13
21-25	33.12 \pm 5.97	31.88 \pm 3.04
26-30	43.34 \pm 2.30	31.12 \pm 2.61
31-35	35.94 \pm 1.28	37.16 \pm 2.33
36-40	34.94 \pm 1.03	39.22 \pm 1.91
40-45	36.90 \pm .62	36.88 \pm 1.73
<i>Phase G</i>		
1-5	27.65 \pm 1.28	39.36 \pm 2.52
6-10	35.81 \pm 2.01	35.54 \pm 4.91

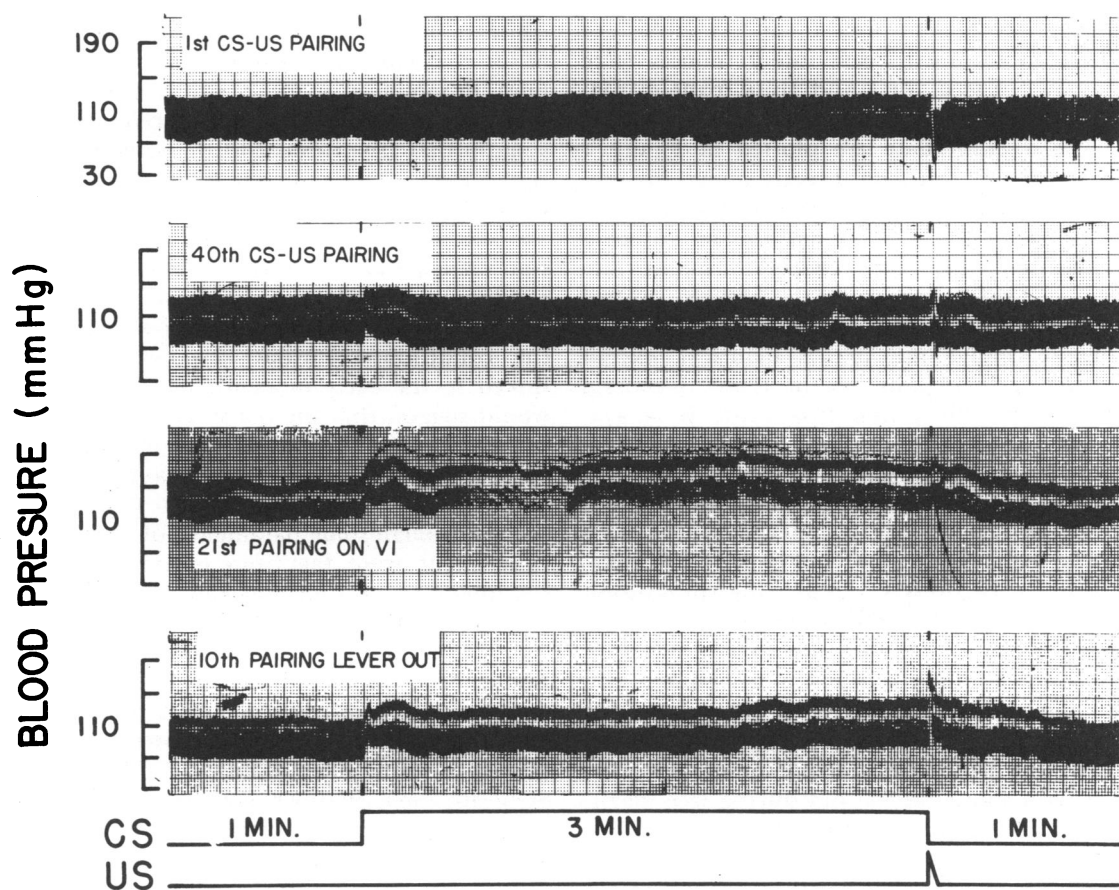


Fig. 2. Strip-chart blood pressure recordings of Monkey P during selected trials as indicated in the inserts. Each record is 5 mins long and is centered on the 3-min CS. Pressure measurements were made with a strain-gauge transducer attached to a catheter implanted into the descending aorta via the femoral artery. Catheter length was approximately 60 cm.

that an increased cardiac rate is the primary mechanism responsible for conditioned, anticipatory blood pressure elevations [e.g., Smith & Stebbins, 1965; Stebbins & Smith, 1964]. With close inspection, this can be verified in Figure 2.) When superimposed on operant responding and accompanied by behavioral suppression, the CS elicited a larger magnitude cardiovascular response which was sustained throughout the CS (third record). Note also in this record the high frequency component riding on the systolic pressure wave. Finally, the effect was partially reversible. When pairings were again carried out on a background of no, or only informal, instrumental activity, the cardiovascular response was reduced, although not to its original level or brevity.

Figure 3 presents the data for Monkey T in the same format as Figure 1 except for the omission of an uneventful operant training

phase. The principal findings described above were fully replicated with larger, 20 to 30 bpm, heart rate accelerations occurring exclusively during trials superimposed on schedule-controlled responding for food, and not during free meals. Also, as before, the modulating effects of the two behavioral backgrounds appeared reversible as the lever was removed from the chamber for ten sessions (second panel from right) and then replaced (far right panel). Of particular interest in Monkey T's data is the clear evidence that during the first 15 on-baseline trials total suppression of operant responding well preceded the ultimate development of large magnitude, anticipatory heart rate changes during the CS. Thus, behavioral and cardiac conditioned responses were found to be dissociated from one another across, as well as within, CS presentations. Like Monkey P, this subject also showed an even-

tual temporal discrimination of the CS interval in terms of operant suppression, coupled with the reverse heart rate pattern of greater conditioned acceleration during the initial CS minutes.

The control heart rates in Figures 1 and 3 suggest that for neither subject could the enhancement of conditioned cardiac responses during operant performance be explained in terms of lowered control rates. Control heart rates were normally equal, and sometimes higher, during operant sessions than during sessions when food was freely available. In turn, the heart rates during both types of sessions were routinely higher than resting levels between sessions when no food was present. In particular, the data of Monkey P in Figure 1 during the final reversals between operant and "lever-out" sessions show that the augmented cardiac responses during the former were not attributable to a "law of initial values." Control heart rates were always higher and accelerations during the first CS

minute always greater during operant sessions. There was no overlap between operant and nonoperant sessions in these data.

During the operant training phase, the control heart rates of both monkeys showed transient fluctuations with each change in the schedule of reinforcement similar to the results reported for squirrel monkeys (*Saimiri sciureus*) by Morse, Herd, Kelleher, and Grose (1971). For example, following 10 sessions of continuously reinforced responding, the heart rates of both monkeys rose sharply when the slight random ratio requirement, $P = .5$, was introduced. Even though both subjects were easily able to obtain as much food as in prior sessions, Monkey P's heart rate increased from 176 beats per min (mean of 10 sessions hours) to 220 (mean of 1 hr), and Monkey T's from 184 to 211. In following sessions, the random ratio requirement was made progressively more stringent, and, despite steadily increasing response rates and decreasing reinforcement rates, neither monkey's heart rate again

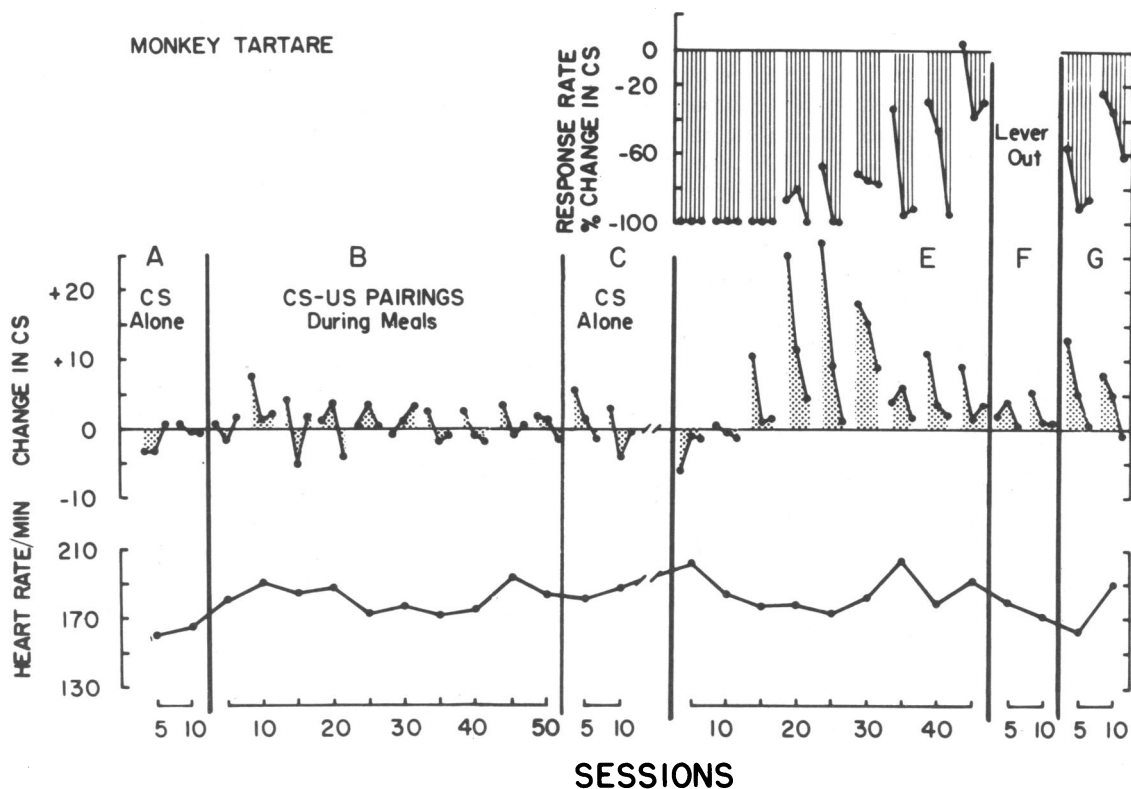


Fig. 3. Monkey T's control heart rates (bottom) and minute-by-minute deviations during the CS in both heart rate (middle) and operant response rate (top) in successive phases of the experiment. The data are averaged in 5-session blocks and the format is the same as in Figure 1 except that the operant training phase (D) has been omitted.

matched the tachycardia prompted by the initial introduction of an intermittent contingency.

DISCUSSION

The principal findings of the present experiment were twofold. First, the autonomic responses that conditioned to a preaversive stimulus were found to be dissociated from the behaviorally disruptive effects of the same stimulus. As in previous studies, these apparently represent independent properties of the CS, and it is unlikely that either is the sufficient cause of the other. Second, there was a strong interaction between the size of conditioned autonomic responses and the behavioral background upon which they were evoked. Although conditioned suppression and conditioned autonomic responses seemed to condition independently to the same CS-US pairings, they nevertheless interacted strongly.

The importance of situational variables in the formation and maintenance of classically conditioned responses has long been recognized, most often anecdotally. Pavlov noted that the presence of an unfamiliar experimenter or the absence of a familiar chair in the experimental chamber could enhance or inhibit an already established CR (Wyrwicka, 1972, pp. 36-37). The peculiar salience of normally unprogrammed situational stimuli has also been noted from time to time in the acquisition of autoshaping (Tomie, 1976) and in the formation of operant conditional discriminations (Eckerman, Lanson, & Cumming, 1966). Pharmacological work using the state-dependent learning paradigm has suggested that even interoceptive contextual stimuli involving broad, but non-debilitating, bodily changes within the subject itself can modify both the course of learning and its level of performance, as well as serve as discriminative cues in the formal sense (Overton, 1966). The additional suggestion of the present experiment is that the subject's own behavior may also form part of the "situation" to which concurrent classically conditioned respondents are sensitive. Just as conditioned responses may be dependent on both exteroceptive and interoceptive contextual variables, the current data can be interpreted to suggest that changes in the subject's own operant behavior may similarly come to interact with concurrently conditioned auto-

nomic responses, even when the former are induced by the same environmental events that prompt the latter.

The question naturally arises as to what mechanism the enhanced conditionability of cardiovascular respondents during operant suppression can be attributed. This question may be premature since it is not certain in the present experiment which were the key parameters of the on- vs. off-baseline procedures responsible for the modulation of conditioned autonomic responses. It seems clear that operant suppression per se was neither the necessary nor sufficient cause of the increased cardiac responses during the operant phases, E and G, of the experiment. For, consistent with prior observations (Brady et al., 1969), suppression and the conditioned autonomic events were fully dissociable both within and across trials. Moreover, studies of positive conditioned suppression in monkeys have shown that no discernible cardiovascular conditioned responses are elicited by CSs when the latter stimuli signal free food instead of shock (Kelly, 1973a, Note 1). So while both prereward and preaversive stimuli appear capable of suppressing ongoing operant behavior, only preaversive stimuli have been consistently correlated with conditioned cardiovascular responses. Hence, it would seem that the occurrence of operant suppression per se during phases E and G of the experiment was insufficient to account for the augmented cardiovascular respondents.

In a similar vein, one might be tempted to argue that the enhanced magnitude of autonomic responses during concurrent operant sessions reflected the greater cost to the subject in terms of the reinforcements missed during the suppression occasioned by the preaversive CS. However, it is known that discriminated extinction, or timeout, stimuli which explicitly signal the unavailability of reinforcement do not by themselves elicit conditioned cardiovascular effects in monkeys at parameters identical to those in the present experiment (Brady et al., 1969; Kelly, 1973a, Note 1). Extinction-correlated and preaversive stimuli differ in other ways, however, which may also be related to their differential cardiovascular effects. While it is true that both are accompanied by a reduction in reinforcement frequency, extinction stimuli are also correlated with the cancellation of the response contingency, or of the organism's opportunity to

respond for reinforcers. Perhaps reinforcers are "missed" more during preaversive stimuli when changes in the subject's own behavior play a role in their reduction.

Another, somewhat more plausible, interpretation of these findings is that enhanced preaversive respondents during concurrent operant performance may simply reflect the heightened discriminability of the CS consequent to the greater response-produced feedback from the behavioral suppression itself. Such behaviorally generated stimuli would become part of the preshock stimulus compound and might have strong salience for the subject. The sequence of this stimulus compounding would run as follows. The preaversive CS during on- but not off-baseline sessions results in operant suppression, feedback from which would become part of the stimulus complex preceding shock. Since these interoceptive stimuli are themselves subsequently paired with shock, they theoretically at least could affect the conditioning of autonomic respondents, a process that, as mentioned above, appears to proceed independently of conditioned suppression. The assumption here is that behaviorally generated stimuli as part of the preaversive CS compound might augment the conditioning of autonomic response by virtue of their greater salience for the organism relative to the exteroceptive stimuli programmed by the experimenter.

One complication in viewing the suppression induced by a CS as part of the CS itself is that such internal feedback must be considered a novel stimulus to the subject, compared to its prior more extensive history with the exteroceptive CS. Most novel stimuli prompt unconditioned cardiovascular responses on their own part unless the subject has been previously habituated to them. Thus, just on the basis of its novel stimulus value, internal feedback from newly conditioned suppression could bias the subject toward larger autonomic responses during operant sessions than might be expected when the exteroceptive CS was delivered when the subject was idle. Were this interpretation correct, one might predict that the strength of autonomic responses should be proportional to the severity of operant suppression, because the more severe the suppression on early trials the more intense the novel feedback stimuli. The evidence, however, is otherwise. Figure 3 demonstrated

that during the first 15 on-baseline trials, total suppression of operant responding well preceded the development of large magnitude anticipatory heart rate changes during the CS. This would suggest that an unconditioned novelty effect, if any, of interoceptive stimuli correlated with suppression did not play a large role in the modulation of conditioned cardiovascular responses. Rather, the time course of these changes suggest that if internal feedback from suppression did subsequently become part of the CS complex, its respondent-eliciting properties appear to have been acquired gradually over trials in the manner of a simple associative process.

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